Seasonal changes in shoot and root production and in carbohydrate content of salmonberry (*Rubus spectabilis*) rhizome segments from the central Oregon Coast Ranges

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An extensive rhizome system is an important aspect of the morphology and architecture of salmonberry (*Rubus spectabilis* Pursh) and of its potential for regrowth following disturbance. Seasonal activity of the rhizome system was studied by collecting rhizome segments monthly from February through October 1988 and February 1989 from four sites. Total nonstructural carbohydrate content was determined and segments were incubated in a growth chamber to determine periodicity of shoot and root production. The number and dry weight of shoots peaked in February and March, declined from April through June when aboveground shoot growth was greatest and were generally low through the dry summer months. Root production was highest from August through October and generally lower the rest of the year. Total nonstructural carbohydrate content was highest during the dormant season and dropped to the lowest level in midsummer. Shoot production was more closely associated with total nonstructural carbohydrate content than was root production. The significant reduction in shoot production potential suggests a time in the annual growth cycle when the species capacity for regrowth following disturbance is at a relatively low level.

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Un système bien développé de rhizome est une caractéristique importante de la morphologie et de l'architecture de la ronce remarquable (*Rubus spectabilis* Pursh) et de sa capacité à se régénérer suite à une perturbation. L'activité saisonnière du système de rhizome a été étudiée en prélevant des segments de rhizome à chaque mois, du mois de février au mois d'octobre de 1988 et au mois de février de 1989, dans quatre sites. Le contenu en total en hydrates de carbone non structuraux a été mesuré et les segments furent incubés dans des chambres de croissance pour déterminer la périodicité de la production de racines et de tiges. Le nombre et le poids sec de tiges a atteint un sommet en février et mars, a diminué par la suite d'avril à juin alors que la croissance aérienne de la tige était maximale et a généralement été faible pendant les mois secs d'été. La production de racines était maximale du mois d'août au mois d'octobre et généralement plus faible le reste de l'année. Le contenu en total en hydrates de carbone non structuraux était le plus élevé pendant la saison de dormance et diminuait au niveau le plus faible au milieu de l'été. La production de tiges était plus étroitement reliée au contenu en total en hydrates de carbone non structuraux que la production de racines. La forte réduction de la capacité à produire des tiges suggère qu'il y a un moment dans le cycle annuel de croissance où la capacité de l'espèce à se régénérer, suite à une perturbation, est à un niveau relativement faible.

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Introduction

Salmonberry (*Rubus spectabilis* Pursh) is a common understory shrub in coastal forests from Oregon to southeastern Alaska. It occurs on moist sites and can persist indefinitely in the understory of both hardwood and conifer stands (Newton et al. 1968; Barber 1976; Carlton 1988; Tappeiner et al. 1991). Its persistance results from a combination of a buried seed bank and a bud bank. Seed quantity can be great in undisturbed stands and seedling density can be high following disturbance of the forest floor and surface mineral

soil (Ruth 1970; Barber 1976; Maxwell 1990; Tappeiner and Zasada 1993). However, seedlings grow more slowly than shoots originating from the bud bank and, although important, they are not the basis for the rapid regrowth of salmonberry following disturbance. The bud bank occurs on aboveground stems, and an extensive rhizome system (Barber 1976; Maxwell 1990; Tappeiner et al. 1991; Zasada et al. 1992). Shoots developing from these buds have the capacity to grow rapidly and to quickly occupy growing space made available by a disturbance. All types of buds can produce new shoots whether they occur on intact or fragmented clones or rhizomes.

Salmonberry clones consist of a network of rhizomes with 1–50 or more aerial stems distributed at intervals of up to 2 m; clone size is negatively correlated with overstory density. Dense populations of salmonberry may consist of one or more clones. Aerial stem densities of 2–10/m^2 are common in undisturbed stands; below ground, up to 10 m/m^2 of rhizome may occur. Following natural or human-caused disturbance, buds on rhizomes and at the base of aerial stems are activated. Density of new stems can increase dramatically following disturbance; new rhizomes in disturbed areas can be two to five times greater than in undisturbed stands (Tappeiner et al. 1991; Zasada et al. 1992).

Increased density of salmonberry after timber harvesting impedes conifer regeneration (Wagner 1989; Tappeiner et al. 1991; Zasada et al. 1992). Seedling growth is often decreased and, if competition from salmonberry is severe, regeneration will fail to become established (Chan and Walstad 1987; Wagner 1989).

Because salmonberry is an important species in ecosystem structure and function in coastal forests and a potential hindrance to conifer regeneration much has been done in recent years to learn more about how to manage this species to meet a variety of forest ecosystem management objectives (Wagner 1989; Maxwell 1990; Tappeiner et al. 1991; Zasada et al. 1992; Maxwell et al. 1993; Tappeiner and Zasada 1993). To better understand the dynamics of salmonberry regrowth after disturbance, we conducted a study to determine the seasonal variation in the production of shoots and roots from salmonberry rhizome segments and the association of that production with carbohydrate reserves.

Methods

Study sites

Four clear-cut sites in the Oregon Coast Ranges on the Waldport and Hebo Ranger Districts of the Siuslaw National Forest were studied. An unburned site and a site that had been broadcast burned for slash reduction and control of competing vegetation were located on each district. The Waldport District sites were immediately next to each other, but separated by a seasonal stream channel, in a midslope position with a west aspect. The Hebo District sites were on adjacent ridges, in a mid to upper slope position with a southwest aspect. Each site was harvested 1–2 years before the study and burned in the spring or fall after harvest. The sites were representative of those needing treatment to reduce salmonberry competition for 1- to 2-year-old, planted Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings.

Shoot and root production

Within each site, a 0.5- to 1.0-ha area of uniform slope and aspect was selected for rhizome collection on each of 10 sampling dates (monthly from February through October 1988 and in February 1989). The sites on each district were sampled on con-

secutive days. Rhizome samples were collected from 5–10 clones on each sampling date (see Tappeiner et al. (1991) and Zasada et al. (1992) for a description of salmonberry clones). A sample for a given site consisted of 12–20 m of rhizome material. Rhizomes were collected from all rhizome diameter classes (1–3 cm) that have been observed to produce shoots under field and laboratory conditions. The only portions of a rhizome not utilized were the 15–20 cm portion proximal to the apical meristem of the rhizome and severely damaged sections.

Following removal from the soil, rhizome segments (>20 cm long) were placed in plastic bags and stored in ice in an insulated cooler; about 5 h elapsed between the time sections were collected and the time they were prepared for incubation. In the laboratory, soil was washed from the sections, all roots were removed and the sections were cut into 20-cm segments. A segment length of 20 cm was selected as the basic sample unit based on previous exploratory studies and general knowledge of node density on rhizomes. We could not standardize rhizomes by the number of stem units (node plus associated internode) because visible external signs of node identity disappear within a year or less of rhizome formation and most of the rhizome system is comprised of material older than that. We could have restricted the rhizome population to only those rhizomes with easily identifiable nodes, but they represent 20% or less of the rhizome system that has the potential for producing shoots (Tappeiner et al. 1991). Rhizome segments used in this study had no visible sign of bud activity before they were placed in the incubator. Segments from all parts of the rhizome system were pooled in our study as an earlier study (Maxwell 1990) did not find any significant effect of original position of the segment in the intact clone on activity of segments when detached from the clone.

The 20-cm segments were incubated in 24 × 28 × 4 cm plastic boxes (Wang and Ackerman 1983). Each box had a tray that elevated the segments about 1 cm above the bottom and permitted excess water to drain away from the segments. The tray was covered with two layers of cellulose germination pad (about 0.5-cm thick when dry). Twelve segments were placed on the pad and completely covered with an additional two layers of pad. Each collection date–site combination consisted of five boxes of 12 segments for a total of 60 segments for each test; approximately 2000 segments were included in the study. After placement in the boxes, the segments were soaked in water at room temperature for 24 h, drained, and placed in the growth chamber. The boxes were incubated in the dark with a 15:10°C temperature regime (16:8 h). Preliminary tests had indicated that this regime resulted in a more rapid appearance of shoots, but not in greater shoot production than incubation at constant temperatures of either 15 or 10°C (Maxwell 1990). Rhizomes were checked weekly and watered as necessary.

At the end of the 55-day incubation period, the rhizome segments were removed from the trays, and the number of active buds, shoots, and roots were counted. Active buds included shoots and buds. Shoots were defined as those active buds that exhibited measurable internode elongation either with expanded leaves or without. Buds appeared as expanded axillary buds or secondary buds; the scales of these buds were still intact and there was no visible internode elongation. These buds were not visible when incubation began. Length of the longest shoot on each segment was measured. Dry weight of shoots produced by a segment was determined after drying for 48 h at 65°C.

Carbohydrate analysis

Rhizome samples for analysis of total nonstructural carbohydrates (TNC) were collected as described above for the incubation studies. A sample for TNC analysis consisted of a subsample from all rhizomes collected from a site on a given date. Three subsamples were analyzed on each date of collection. Rhizomes were thoroughly washed, cut into small pieces, dried at 65°C for 48 h, ground to pass a 20-mesh screen and stored

TABLE 1. Analysis of variance tables for shoot and root production by rhizome segments and TNC of salmonberry rhizome segments

Source of variation[a]	df	SS	MS	F	$p > F$
% active buds					
T	1	13.82	13.82	0.02	0.919
D	9	3 602.62	400.29	1.25	0.325
T×D	9	2 230.05	247.78	0.78	0.640
% shoot					
T	1	386.38	386.38	0.35	0.659
D	9	21 104.75	2344.97	3.29	0.015
T×D	9	4 135.90	459.54	0.65	0.745
% root					
T	1	488.82	488.82	0.11	0.659
D	9	83 870.43	9207.83	6.49	<0.001
T×D	9	2 693.96	299.33	0.21	0.989
No. of buds					
T	1	0.28	0.28	0.05	0.866
D	9	77.46	8.61	1.85	0.127
T×D	9	22.69	2.52	0.54	0.825
No. of shoots					
T	1	0.24	0.24	0.05	0.866
D	9	127.49	14.17	7.58	<0.001
T×D	9	4.83	0.54	0.29	0.970
No. of roots					
T	1	97.30	97.30	2.05	0.388
D	9	1 211.33	134.59	3.49	0.012
T×D	9	111.75	12.42	0.32	0.957
Dry weight					
T	1	0.21	0.21	2.29	0.372
D	9	5.50	0.61	5.67	0.001
T×D	9	0.95	0.11	0.98	0.490
TNC					
T	1	3.35	3.35	0.68	0.562
D	9	1 124.00	124.89	70.63	<0.001
T×D	9	26.13	2.90	1.64	0.177

[a]D, date; T, treatment.

in plastic bags at −10°C until analyzed. TNC was extracted and hydrolyzed with 0.1 M H_2SO_4 (Smith et al. 1964), and resulting sugars were estimated as glucose (Hassid 1937).

Statistical analysis

The study was a randomized block, split-plot design. The Hebo and Waldport Ranger Districts were treated as blocks with burned and unburned treatments within each block. Burned–unburned treatments constitute whole-plot treatments. Rhizomes were sampled from each whole-plot unit and incubated in the growth chambers. Five subsamples of each date by block by treatment combination were incubated. Dates constituted the split-plot treatments. Data were statistically analyzed with analysis of variance for number of buds, shoots, and roots per rhizome; the percentage of segments with buds, shoots, and roots alone or in combination; average and maximum shoot length per segment; and shoot dry weight per segment. Calculation of means for shoot and root production were based on the number of segments that produced the structures. Statistical analysis of TNC was similar to that for root and shoot regrowth except that there were three subsamples from each collection date in the analysis.

Results and discussion

Salmonberry rhizome segments readily produced shoots and roots. Neither burned–unburned sites or geographic area (i.e., ranger district) differed ($p < 0.10$) in any of the vari-
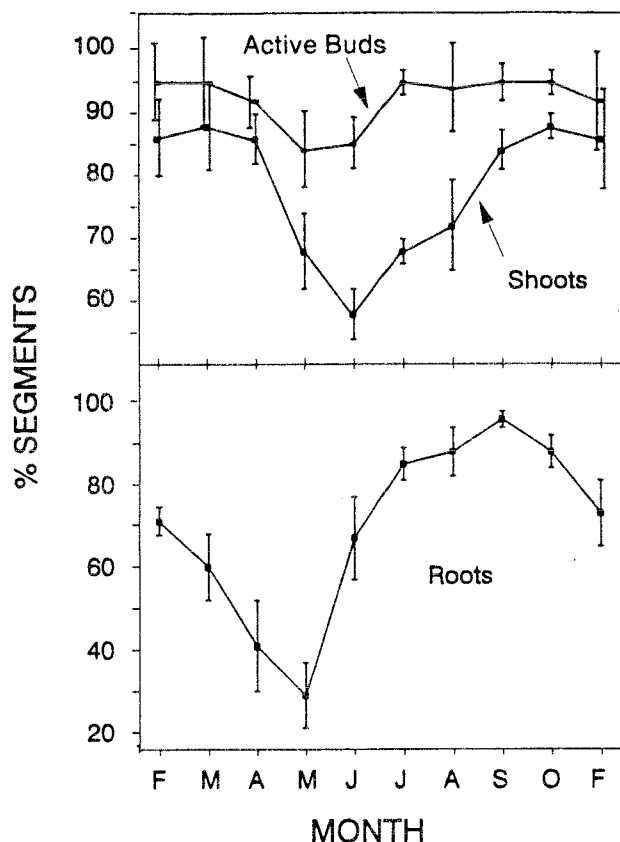

FIG. 1. The percentage of rhizome segments that produced active buds, shoots, and roots. Segments were collected from intact salmonberry clones on four sites monthly from February through October 1988, and in February 1989.

ables used to quantify rhizome activity (Table 1); therefore, data for all sites were combined for statistical analysis. However because of the relatively small sample of these variables in this study, we cannot conclude that prescribed fire and geographic location have no effect on the activity of rhizome segments.

Analysis of the combined data indicated that time of year when rhizomes were collected had a significant effect on the proportion of segments (percent production) producing active buds, shoots, and roots (Table 1). The period of lowest percent production of shoots was from May to August (Fig. 1). The low point in percent production of roots, April and May, was earlier than that for shoots. Twenty-five percent of the segments produced roots in May when root development was lowest, but the percent production of shoots did not drop below about 60% (Fig. 1). When all activity (segments with at least one active bud or root) was considered, the lowest percent production was 90%, indicating that the majority of segments showed some activity regardless of the time of year when collected.

Time of collection significantly affected total number of active buds, number of shoots, dry weight and length of shoots, and the number of roots produced per rhizome section (Table 1, Fig. 2). The average number of active buds per section ranged from about 3 to 8 per 20-cm segment. The maximum number of active buds on a segment was 28 or about 1.4 buds/cm. The percentage of active buds that elongated into shoots ranged from 37 to 58%; lowest percentages were in the July to October period. Average root production
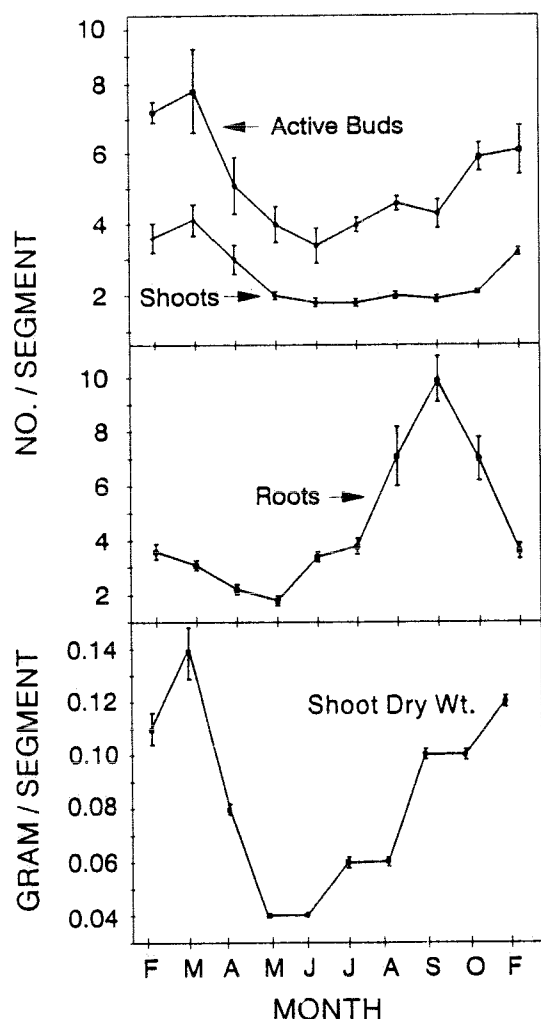
FIG. 2. The number of active buds, shoots, and roots, and shoot dry weight, produced by rhizome segments removed from intact salmonberry clones at different times of the annual growth cycle.
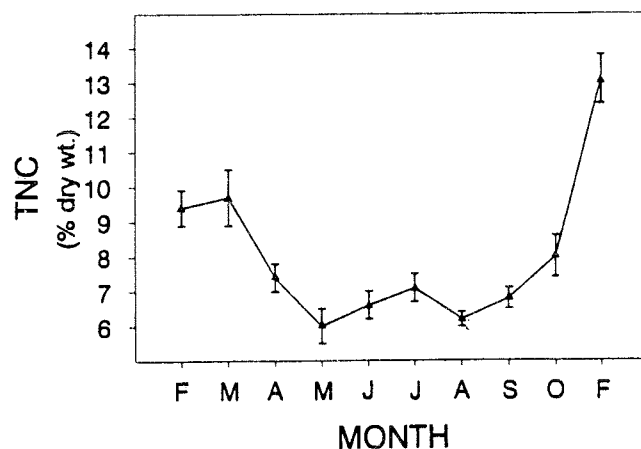

FIG. 3. Total nonstructural carbohydrate content (TNC) of salmonberry rhizome segments removed from intact clones at different times of the annual growth cycle.

ranged from 2 to 10 roots per segment (Fig. 2). Maximum root production occurred from August through October, and minimum from February to July.

There was no difference among collection dates and sites in the time required for the first shoots and roots to appear. In general, signs of bud expansion were apparent after 1 week of incubation. The first shoots appeared after 7–14 days of incubation; the first roots after 14–21 days.

The decline in shoot production was associated with the period of most rapid shoot elongation under the environmental conditions extant at the study sites. Bud break in the field occurred in early March, but the first measurable shoot elongation did not occur until early April. Elongation in April, May, and June was 38, 47, and 15%, respectively, of total seasonal shoot elongation. Some elongation was observed on isolated plants in July and August, but, in general, salmonberry shoot elongation did not occur at this time. May and June were also the time of fruit growth and ripening, processes that also require energy from stored reserves or current photosynthate. The dates for elongation and fruit development generally corresponded to observations reported by Maxwell (1990) on similar Coast Range sites. Barber (1976), working in forested areas about 500 km

north of our sites, observed that no shoot elongation occurred until May; growth in May, June, and July contributed 30, 42, and 28%, respectively, of total annual shoot elongation.

The seasonal pattern of rhizome shoot production observed in our study (Figs. 1 and 2) was similar to other species that produce shoots from rhizome and root segments. This pattern has been observed in balsam poplar (*Populus balsamifera* L.) and aspen (*Populus tremuloides* Michx.), both of which form shoots from root segments, and in *Calamagrostis canadensis* Michx., a rhizomatous grass (Schier and Zasada 1973; Schier and Campbell 1976; Krasny 1986; Hogg and Lieffers 1991). In aspen, the number of shoots produced did not differ between dormant and growing season samples although the dry weight of shoots differed among collection dates (Schier and Zasada 1973). In salmonberry and balsam poplar, both measures of shoot production differed. Other types of cell division and growth may also occur when root or rhizome segments are incubated. For example, in aspen and balsam poplar, root segments produced undifferentiated callus at the cut ends (Schier and Campbell 1976; Zasada et al. 1981). No callus formation was observed on salmonberry rhizomes in our study.

The ability of root and rhizome segments to produce new roots after separation from the parent plant differs among woody plants. Salmonberry, rose (rhizomes), and balsam poplar (roots) have a high capacity to initiate new roots from excised segments. In these species, 90–100% of rhizome or root segments produced roots at one or more sample dates during the year (Schier and Campbell 1976; Zasada et al. 1981; Calmes and Zasada 1982). In contrast, aspen root segments and rhizome segments of Gambel oak (*Quercus gambelii* Nutt.) and chokecherry (*Prunus virginiana* L.) have an apparently low potential or inability to produce new roots on incubated segments (Schier 1983).

Two types of roots can develop on salmonberry rhizomes. These are roots that form in association with nodes and are a direct result of activity of the apical meristem of the rhizome and adventitious roots that are not associated with the nodes. In our study, only adventitious roots were produced and the point of root origin appeared unrelated to position of nodes or the location or roots clipped before incubation.

The quantity of TNC was significantly affected by time of collection and the average for all sites ranged from 5 to

14% of rhizome dry weight (Table 1, Fig. 3). The period of TNC accumulation in the rhizomes occurred between the October and February sampling dates when TNC concentration doubled (Fig. 3). Leaves had senesced by October, and the plants were leafless from early November to the sampling date in February. Barber (1976) observed sharp decreases in salmonberry rhizome carbohydrate content during periods of maximum shoot and root development. The general pattern of TNC content (Fig. 3) has been reported for the roots and rhizomes of a number of plant species (Schier and Zasada 1973; Roper et al. 1988; Keller and Loescher 1989; Hogg and Lieffers 1991; Dickson 1991). The timing of fluctuations in the annual cycle of TNC differs among species owing to inherent patterns of development and growing season conditions.

The seasonal patterns of shoot production, shoot dry weight, and TNC content were similar. The main deviation from an identical pattern was the greater shoot dry weight from June through October before TNC began to increase (Figs. 2 and 3). The relationship between TNC and shoot production variables found for salmonberry in this study differed from that in aspen. In aspen, the number of shoots was not related to TNC, but the dry weight of the shoots was related (Schier and Zasada 1973). Other physiological and environmental factors interact with TNC in determining shoot growth. Schier (1973, 1981) and Nissen and Foley (1987) have shown the importance of various plant hormones in the regulation of shoot production by root and rhizome systems. Schier (1972) found that apical dominance is quickly re-established by the first new shoots developing on aspen root segments, and this significantly reduces the number of shoots produced from the potential bud population. This effect probably accounts for our observation that only 37–58% of the active buds developed into shoots. Hogg and Lieffers (1991) found that incorporating rhizome nitrogen content and TNC into a model for predicting *Calamagrostis* regrowth from rhizome segments produced better estimates than models using only rhizome TNC.

Root production was somewhat out of phase with TNC content. Production dropped by about 50% between February and May and was lowest when TNC was at the lowest annual level. Root number, however, was greatest when TNC levels were low (Figs. 2 and 3). The highest TNC levels were not associated with the highest levels of root production. An inverse relationship between root production and carbohydrate content in grass rhizomes has been reported by Ferreira and Valio (1992) and this relationship seems to hold to some degree in salmonberry rhizomes as well.

The results of our study and other work (Barber 1976; Maxwell 1990; Tappeiner et al. 1991) provide insight into the potential activity of the salmonberry rhizome bud tank following disturbance. Unpublished data from other work that we are doing on salmonberry indicates that, on average, there are about 56 buds/m of rhizome. Using alder stands as an example, rhizome length was reported to range from 2.5 to 8.0 m/m^2 (Tappeiner et al. 1991). These two estimates suggest a bud density of 140–448 buds/m^2. Estimates from this study (using March data as an example) indicate that about 20 buds/m of rhizome, 4–14% of the bud population, might produce shoots immediately after a disturbance.

Practical implications

This study has implications for land managers concerned with salmonberry regrowth after disturbance. First, our study

and those by Barber (1976) and Maxwell (1990) provide documentation for the commonly held belief that salmonberry is highly resilient to disturbance, even if the disturbance results in fragmented clones. Second, if it is necessary to propagate salmonberry on areas where it does not occur, use of rhizome segments provides an excellent and dependable means of plant production. This could be important in riparian areas where streamside vegetation has been destroyed. Finally, the association of low shoot production with low levels of TNC suggests that the period from May through July, and perhaps even into October, may be a time when salmonberry is more susceptible to physical disturbance. Unpublished results from a study of the response of salmonberry to manual cutting indicated that treating salmonberry within the May to June period can reduce the rate of stem height regrowth during the current and following growing season.

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